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Importance of Seed [Fe] for Improved Agronomic Performance and Efficient Genotype Selection

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1. Introduction

Plants require a continuous supply of iron (Fe) to maintain proper growth. Although the most abundant micronutrient in surface soils (Fageria et al., 2002), Fe is the most limiting to agricultural production throughout the world (Kochian, 2000) and to soybean production in the North Central United States (Hansen et al., 2003). Iron deficiency is a complex disorder and occurs in response to multiple soil, environmental, and genetic factors. Iron deficiency chlorosis (IDC) is symptomatic of the disorder and commonly observed on high pH, highly calcareous soils. Planting Fe deficiency- resistant soybean [*Glycine max.* (L.) Merr.] varieties has been promoted as the best strategy to alleviate or avoid Fe deficiency where soybean is grown on high pH, highly-calcareous soils (Fairbanks et al., 1987; Goos and Johnson, 2000; Naeve and Rehm, 2006). However, screening nurseries used to identify more resistant varieties based on visual chlorosis scores (VCS) do not always provide consistent, reliable results. A major obstacle to breeding for Fe chlorosis resistance in soybean has been that Fe deficiency symptoms and resistance scores cannot be consistently replicated among experiments. Inconsistent results preclude precise recommendations. Naeve and Rehm (2006), using nine highly tolerant and one moderately tolerant genotype, concluded that variety evaluation for IDC must be done at multiple IDC prone locations with varying soil chemical factors. One hypothesis is that this lack of consistency is probably due to the complex chemical and physical criteria in both the plant and soil that must be met for chlorosis to occur (Fairbanks, 2000; Naeve and Rehm, 2006). A more accurate and precise estimate of resistance to Fe deficiency may be expressed by a different plant character.

Ideally, plant traits measured to characterize resistance to Fe deficiency would be accurate, precise, simple, rapid, and inexpensive. Few plant traits or measures satisfy all of these requirements. For resistance to Fe deficiency, the "measure of choice" for decades (Weiss, 1943; Cianzio et al., 1979; Froehlich and Fehr, 1981; Fairbanks et al., 1987; Penas, et al., 1990; Goos and Johnson, 2000; Helms et al., 2010) has been a subjective, discontinuous, visual estimate of the degree of chlorosis, i.e. VCS, of the most recently fully-expanded middle leaflet of the third or developmentally younger trifoliolate. Cianzio et al. (1979) concluded that evaluation of foliar chlorosis, rather than measurement of chlorophyll concentration, is the most efficient procedure for comparison of cultivars because it requires relatively less labor. However, visual estimates of chlorosis when only the first trifoliolate leaf is fully

developed (Cianzio et al. 1979) may be more a reflection of planting seed [Fe][1] than resistance to Fe deficiency (Ambler and Brown, 1974; Tiffin and Chaney, 1973; Chaney et al., 1992). Furthermore, Naeve and Rehm (2006) concluded that varietal screening based on VCS likely requires that evaluation is conducted at multiple locations to be predictive. This suggests that using VCS to identify more resistant cultivars may not be the most efficient or least expensive procedure. It has been suggested that the plant character (plant height, seed number, grain yield, seed [Fe], VCS, relative chlorophyll [SPAD] reading) used to measure Fe deficiency is of primary importance in the classification of genotypes for resistance to Fe deficiency (Wiersma, 2007). Many of the characters mentioned are known to vary markedly in screening nurseries as well as in management studies (Helms et al., 2010; Naeve and Rehm, 2006; Wiersma, 2005, 2007, and 2010).

In measuring the indirect effects of recurrent selection for Fe efficiency in soybean, Beeghly and Fehr (1989) reported that Fe efficiency was not associated closely with grain yield, time of maturity, plant height, seed protein or oil, leaflet traits, and most micronutrients, except seed [Fe]. Seed weight declined 12%; seed [Fe] increased 13%; whereas, seed Fe content did not change over seven cycles of selection (Beeghly and Fehr, 1989). For soils known to have yield-limiting availabilities of specific micronutrients, increasing the concentration of that micronutrient in seed used for planting has reduced Mo deficiency in corn (*Zea mays* L.) (Weir and Hudson, 1966), Zn deficiency in several species (Rashid and Fox, 1992), Fe and Zn deficiency in rice (*Oryza sativa* L.) (Gregorio et al., 2000), B deficiency in soybean (Rerkasem, et al., 1997), and Fe deficiency in dry bean (*Phaseolus vulgaris* L.) (Beebe et al., 2000) and wheat (*Triticum aestivum* L.) (Shen et al., 2002). Since seed [Fe] can be regarded as an integrated measure of resistance to Fe deficiency that is manifest at maturity, perhaps seed [Fe] should be considered the "measure of choice" in determining susceptibility or resistance to IDC (Bouis et al., 2003; Nestle et al., 2006).

This chapter presents evidence that supports the use of seed [Fe] as an accurate and consistent measure of genotypic differences in Fe efficiency and agronomic performance. This 'evidence' has been garnered from recent soybean Fe deficiency trials conducted on high pH, highly calcareous soils in the North Central region of the USA (Wiersma, 2005, 2007, and 2010), from variety evaluation trials of the Univ. of Minn. Soybean Plant Breeding and Genetics Project, from IDC nurseries managed by R.J. Goos (http://www.soilsci.ndsu.nodak.edu/yellowsoybeans/) and from varietal trials conducted on partially limed and fully limed, acid soils in Brazil (Spehar, 1994).

2. Agronomic performance

Average visual chlorosis scores (VCS) in chlorosis screening nurseries and in management trials involving various treatments are commonly accepted as reasonable estimates of the severity of Fe deficiency. Minor, although statistically significant, differences in VCS observed in the near absence of chlorosis, or in another trial, the near death of many cultivars, have little meaning. In the research discussed here, the severity of Fe deficiency ranged from almost no chlorosis (VCS= 1.2) to mild chlorosis (VCS=2.3) to moderate chlorosis (VCS=3.0) to severe chlorosis (VCS=4.2), nonetheless, consistent genotypic differences usually were observed when genotypes were first grouped into classes based on published VCS, field VCS observed at V3, or planting seed Fe concentration or content.

[1][Fe] is iron concentration.

Class variances were calculated and tested for homogeneity (Snedecor and Cochran, 1980; Gomez and Gomez, 1984) and when class variances were homogeneous, regression equations were developed using class means consisting of both independent and dependent variables. Management studies involving increasing rates of seeding, increasing rates of Fe-EDDHA application, and increasing rates of N application were conducted using resistant, moderately resistant, and susceptible cultivars, without first categorizing the smaller number of genotypes into classes.

2.1 Increasing seeding rates with low Fe-EDDHA rates

It is generally reported that increasing seeding rates will reduce visual chlorosis ratings (early and/or mid-season) and often will increase grain yield when soybean is grown where Fe deficiency is moderate to severe (Uvalle-Bueno and Romero, 1988; Penas et al., 1990; Goos and Johnson, 2001; Lingenfelser et al., 2005; Wiersma, 2007). Increasing seeding density (seeds unit^{-1} of row), and, presumably, increasing the volume of soil occupied by roots unit^{-1} of row, can lead to higher yields and higher seed [Fe]s, but may have little influence on early-season VCS (Fig. 1 A, C, E). When averaged across 3 years, 4 replications, 3 cultivars, and 5 rates of Fe-EDDHA, increasing seeding density almost 3-fold reduced visual chlorosis about 12% (Fig. 1 A). On the other hand, increasing Fe-EDDHA rates (in accordance with the severity of IDC) will markedly reduce early season VCSs, but may have little influence on grain yield (Fig. 1 B, D, F). Averaged across 3 years, 4 replications, 3 cultivars, and 5 seeding densities, increasing the Fe-EDDHA rate 4-fold reduced early season visual chlorosis about 70% (Fig. 1 B). Fe acquisition, measured as seed [Fe], appears to be regulated primarily by genotype, yet Fe acquisition by less Fe-efficient cultivars can be increased by increasing SD or reducing the severity of Fe deficiency. It is possible to slightly increase seed [Fe] of both susceptible and resistant cultivars grown under severe chlorosis if high rates (>4.48 kg ha^{-1}) of Fe-EDDHA are used (Table 1; Fig. 1 F). Rates of Fe-EDDHA used in these studies (Fig. 1) were much lower (1.12 to 4.48 kg ha^{-1}) than those evaluated in other studies (2.24 to 11.2 kg ha^{-1}) and may have been responsible for the moderate responses to increasing rates of Fe-EDDHA.

2.2 High Fe-EDDHA rates

Research to reduce or alleviate IDC in soybean by applying various seed, soil, or foliar Fe chelates or fertilizers has been conducted for decades. Although the results have been mixed (Mortvedt, 1986), and are seldom directly comparable, positive responses to foliar (Randall, 1981), seed (Karkosh et al., 1988), and soil (Penas et al., 1990; Wiersma, 2005) application have been reported. Other researchers have observed only small, if any, response to similar treatments (Goos and Johnson, 2000; Goos and Johnson, 2001; Heitholt et al., 2003). Lack of consistent results may be related to differing levels of chlorosis severity among experiments; soil, environmental, or genetic differences; and/or the low rates of Fe often applied to ensure economic feasibility. Low rates of Fe probably do not satisfy the requirement of a continuous supply of Fe as plant development progresses (Goos and Johnson, 2001).

Responses to higher (beyond economic feasibility) rates of Fe-EDDHA appear variety specific and occur over an extended period, manifest at maturity (Fig. 2). As plant development progresses, there are earlier, limited responses to low rates of Fe-EDDHA, whereas higher rates appear to provide Fe continuously and to promote later, larger responses.

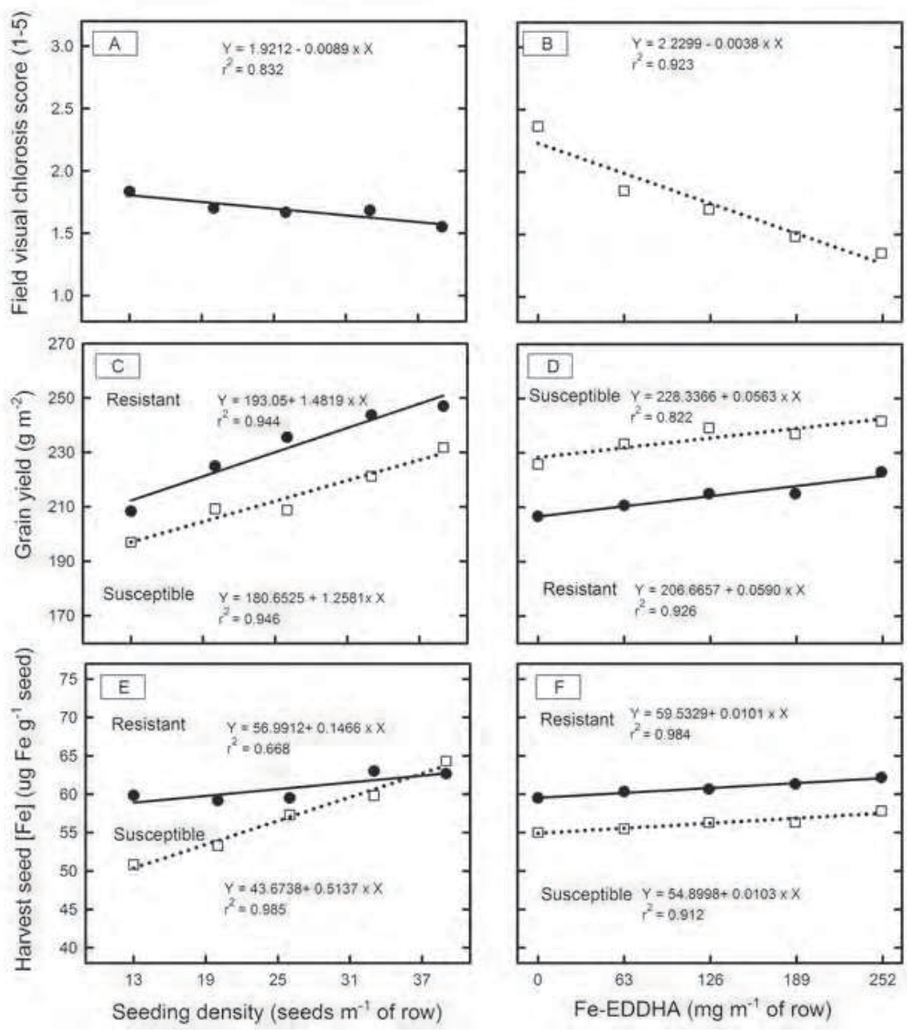

Fig. 1. Visual chlorosis, grain yield, and harvest seed [Fe] of resistant and susceptible cultivars in response to seeding density and Fe-EDDHA rate.

However, it should be noted that the severity of Fe deficiency and the plant characters used to measure treatment response are both crucial when deciding the suitability of various treatments for improving Fe acquisition. For example, measures of field visual chlorosis at low rates of Fe-EDDHA discriminate nicely between resistant and susceptible cultivars, but at higher Fe rates, almost all cultivars have similar scores (Table 1A). In contrast, measures of harvest seed [Fe] provide nearly identical discrimination among cultivars at each rate of Fe-EDDHA, and are nearly the same as the [Fe] of the seed used for planting (Table 1B).

At lower rates of Fe-EDDHA, resistant cultivars often exceed susceptible cultivars in plant height, seed number, and grain yield, whereas at higher rates, susceptible cultivars approach values similar to resistant cultivars (Fig. 2). With only slight chlorosis (Fig. 3, Fisher, MN 2003) seed [Fe] changed very little in response to added Fe for either resistant or susceptible cultivars. With severe chlorosis (Fig. 3, Crookston, MN, 2003), resistant cultivars increased harvest seed [Fe] about 15% in each portion of the canopy, whereas susceptible cultivars changed harvest seed [Fe] little in any portion of the canopy. Harvest seed [Fe]s of

A.

Variety	Initial seed Fe conc.	Fe-EDDHA (kg Fe ha^{-1})						Published chlorosis rating
		0.00	2.24	4.48	6.72	8.96	11.20	
	(µg g^{-1})	field visual chlorosis rating (1-5)						(1-5)
MN0302	88.6	2.1 B†	1.2 A	1.1 A	1.0 A	1.0 A	1.0 A	1.6
GC3104	73.1	3.4 A	1.9 A	1.2 A	1.0 A	1.0 A	1.0 A	2.5
Norpro	91.3	2.6 B	1.4 A	1.2 A	1.0 A	1.0 A	1.0 A	3.3
S2000 2020	57.6	3.8 A	1.5 A	1.1 A	1.0 A	1.0 A	1.0 A	3.7
LSD (0.05)		0.7	NS	NS	.	.	.	
CV		14.9	26	15.7	.	.	.	

B.

Variety	Published chlorosis rating	Fe-EDDHA (kg Fe ha^{-1})						Initial seed Fe conc.
		0.00	2.24	4.48	6.72	8.96	11.20	
	(1-5)	harvest seed [Fe] (µg g^{-1} seed)						(µg g^{-1})
MN0302	2.1 B	64.1 B	64.7 B	66.3 B	66.3 B	77.7 A	74.3 A	88.6
GC3104	3.4 A	42.4 C	49.5 C	47.8 C	51.3 C	53.2 B	52.7 B	73.1
Norpro	2.6 B	79.3 A	77.1 A	78.6 A	76.4 A	76.9 A	80.0 A	91.3
S2000 2020	3.8 A	41.3 C	46.4 C	45.5 C	45.4 C	45.4 B	49.8 B	57.6
LSD (0.05)	0.7	8.3	6.0	5.8	6.3	12.2	9.7	
CV	14.9	9.2	6.3	6.2	6.5	12.0	9.4	

† Means followed by the same letter within a column are not statistically significant at the 5 % level of probability.

Table 1. Field visual chlorosis rating recorded at V3 and seed [Fe] at harvest of four cultivars grown at six rates of Fe-EDDHA applied at planting.

resistant cultivars were consistently higher than that of susceptible cultivars whether chlorosis was nil or severe. This observation is similar to that of Beebe et al. (2000) and Blair et al. (2009) who, from work done with dry beans (*Phaseolus vulgaris* L.), concluded that seed micronutrient densities of Fe (and Zn) were consistent, reliable estimates of resistance to Fe deficiency. Genotypically superior and inferior cultivars could be identified consistently across years and locations (Bouis et al., 2003; Nestle et al., 2006; Ghandilyan et al., 2006). Other research (Wiersma, 2005) has shown that plotting relative grain yield vs seed [Fe] for several environments exhibits a narrow range of seed [Fe] associated with wide ranges in relative yield and that there are consistent seed [Fe] differences between resistant and susceptible cultivars regardless of relative yield. These conclusions have led to the concept that individual genotypes have a seed [Fe] "threshold" that is presumably, genetically

predetermined, yet seldom exceeded, and that seed [Fe] could supplement or replace VCS as a measure of resistance to IDC.

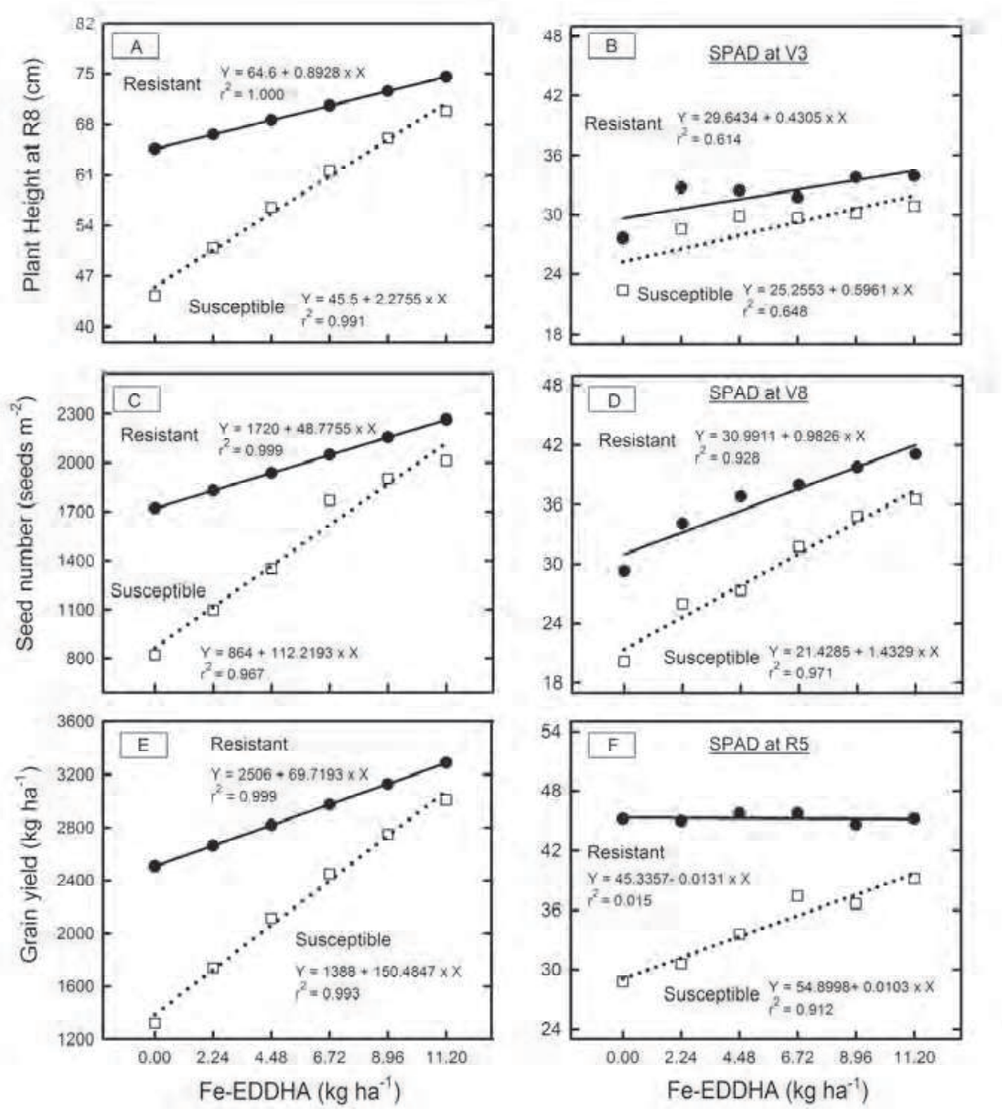

Fig. 2. Agronomic measures of resistance to Fe deficiency in soybean in response to increasing rates of applied Fe-EDDHA averaged over three environments (panels A, C, and E). SPAD measures were recorded at three stages of development in one environment (panels B, D, and F).

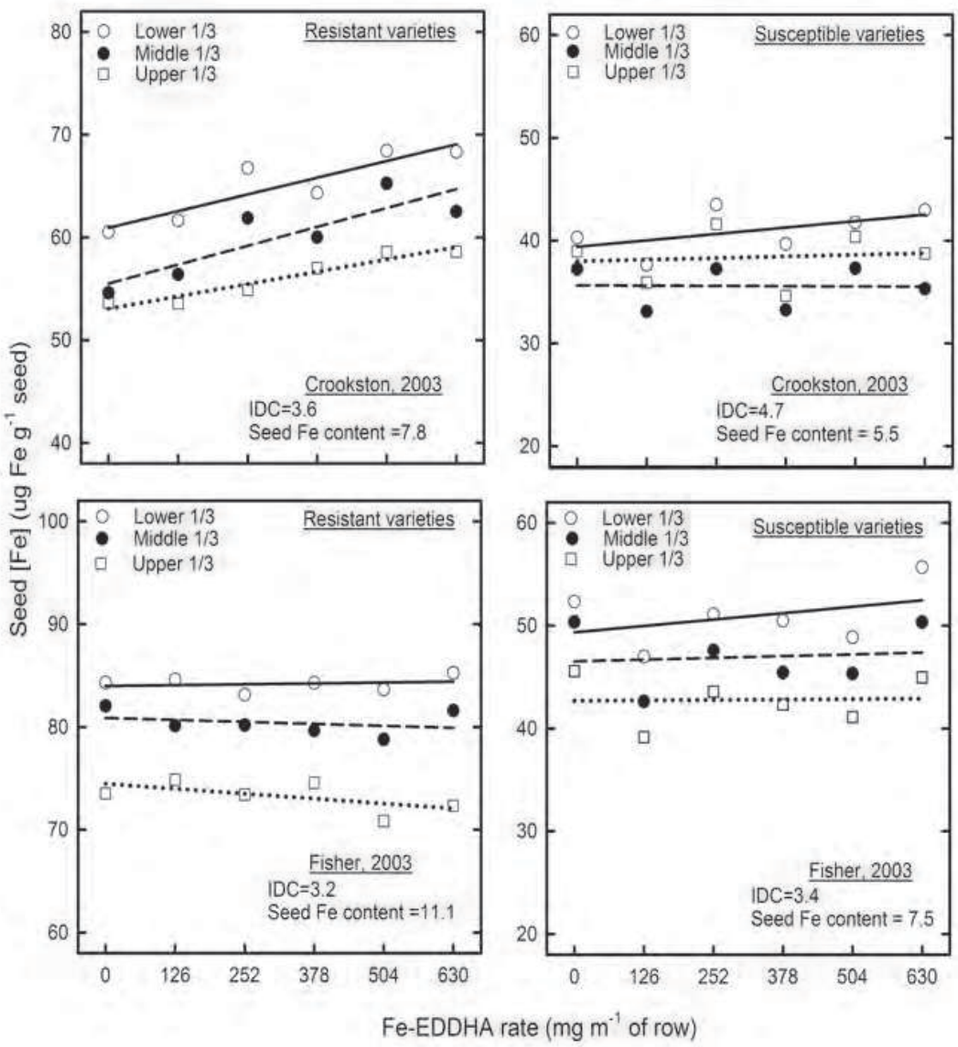

Fig. 3. Seed [Fe] at harvest for different canopy positions of resistant and susceptible cultivars grown under mild to severe Fe deficiency (Crookston, MN, 2003) and nil to mild Fe deficiency (Fisher, MN, 2003).

2.3 Fe-EDDHA rates - canopy position

Ten consecutive plants within row two of each plot in the Fe-EDDHA trials mentioned above were harvested at R7-R8, the total number of main stem nodes was counted, averaged, and used to separate plants into the upper, middle, and lower thirds of the plant. Sections were combined and the number of seeds, total seed weight, and seed [Fe] of the three sections of the canopy were determined. Averaged across cultivars, seed [Fe] decreased from approx. 50 µg g^{-1} at the lower canopy position, to 45 µg g^{-1} in the middle

one-third, to 40 μg g^{-1} in the top one-third (Fig. 3). This decrease occurred under both nil and severe Fe chlorosis and suggests that developmentally younger and older seeds respond similarly to increasing Fe-EDDHA rates. Increases in seed [Fe] occur primarily in resistant cultivars grown under harsh Fe deficiency. Susceptible cultivars show little response to added Fe-EDDHA whether Fe deficiency is nil or severe.

With limited Fe deficiency (Fisher, MN, 2003), both resistant and susceptible cultivars attain their genetically predetermined seed [Fe] (Fig. 3). Taken together, these results suggest that developmentally younger, intermediate, and older seed accumulate Fe at similar rates, but for different lengths of time and that cultivars and canopy positions have very similar regression slopes, but different intercepts or "thresholds" (Fig. 4).

2.4 Nitrogen rates

The response of soybean cultivar resistance to IDC to differing N rates was evaluated in a field study. Six rates of fertilizer N (0, 34, 68, 102, 136, and 170 kg ha^{-1}) were applied to six cultivars differing in resistance to IDC (2 Fe efficient, 2 moderately Fe efficient, and 2 Fe inefficient) over a three year period. Nodulation decreased linearly in response to added N for all cultivars, regardless of their Fe efficiency characterization or yearly growing conditions. In contrast, relative foliar chlorophyll concentrations (SPAD readings) differed markedly among cultivars, but showed little consequential response to increasing nitrogen rates (NR) (Fig. 5). Plant height, seed number, grain yield, and seed [Fe] decreased linearly in response to increasing NRs for Fe-inefficient cultivars, whereas these responses in Fe-efficient and moderately efficient cultivars changed little as NR increased (Figs. 5 and 6). Despite these differences, the ranking of cultivars based on seed [Fe] was only slightly affected by increasing NRs.

3. Genotype selection

When the results of variety evaluations conducted in large-scale chlorosis nurseries are considered, there is little evidence of consequential decreases in VCS among cultivars during the last decade (Fig. 7). However, selecting more resistant genotypes in large screening nurseries is complicated by the large genotype x nursery (environment) interaction, especially where VCSs are used to estimate 'resistance'. Inconsistent variety responses have been attributed to environments, soil heterogeneity, and large variations in soil chemistry (Jolley et al., 1996; Fairbanks, 2000). Ferric chelate reductases and quantitative determination of iron reduction have been suggested as reliable indicators of the genetic potential for chlorosis resistance (Jolley et al., 1996; Fairbanks, 2000). Factors controlling absorption and transport of Fe are known to be located in the root and to be genetically determined (Brown et al., 1958; Brown et al., 1972). Although these measures appear to be reliable, they require specialized equipment and knowledge, limiting the number of potential genotypes that can be evaluated in a reasonable amount of time. Within years, genotypic rank correlations of VCSs (Table 2) are often highly significant across locations, suggesting reasonable reliability. This can be deceiving, however, because large-scale nurseries often have 'normal' distributions with nearly all VCSs being between 2.5 and 3.5 at each location (Fig. 8). In a field study conducted during 2007, 2008, and 2009 rank correlations were calculated among 14 genotypes that had been included each year (Table 5). These results suggest that VCSs may not be the most appropriate measures of Fe efficiency. During the same decade, micronutrient densities (primarily Fe and Zn) in both

grasses and legumes have been found to be reliable and consistent across both years and locations. Research conducted on dry bean (*Phaseolus vulgaris* L.), wheat (*Triticum aestivum* L.), and rice (*Oryza sativa* L.) cultivars demonstrated that genotypes with high micronutrient densities of Fe and Zn during one year at one location will also be among the highest at another location in another year (Gregorio, 2002; Shen et al., 2002; Bouis et al., 2003; Nestle et al., 2006; Blair et al., 2009; Blair et al., 2010). Perhaps, measures of resistance to Fe deficiency in soybean should involve integrated estimates of uptake, transport, and accumulation of Fe that are manifest at maturity, such as Fe content 1000^{-1} seeds, seed [Fe], and/or iron removal with seed (μg Fe m^{-2}).

3.1 Roundup ready vs conventional cultivars

As Roundup Ready™ (RR) cultivars were first being released there was local concern among growers and crop consultants that resistance to Fe deficiency may not have been incorporated during development of earlier releases. During 2002, ten RR™ and ten 'conventional' cultivars were grown at two rates of Fe-EDDHA (0 and 8.96 kg ha^{-1}) at the University of Minnesota Northwest Research and Outreach Center (NWROC) on soils with a known history of mild to severe Fe deficiency. A relatively high rate of application of Fe-EDDHA increased relative chlorophyll readings at V3 about 13% (4.6 SPAD units) and increased grain yield nearly 18% (434 kg ha^{-1}). Roundup Ready cultivars out-yielded conventional cultivars by approximately the same amount, 19% (453 kg ha^{-1}). Nonetheless, seed [Fe] at harvest did not differ between Fe-EDDHA rates, nor between RR and conventional cultivars (Table 3). Seed [Fe] at harvest was moderately related to both published visual chlorosis score (r^2=0.452) and Fe concentration of the seed used for planting (r^2=0.458). Classifying cultivars on the basis of their published VCS and then their planting seed [Fe] resulted in the same cultivars being in each class and, consequently, having the same r^2 values. This research involved a relatively small sample of cultivars grown under harsh conditions and may not have fairly represented the importance of Fe 1000^{-1} seeds, seed [Fe], and/or Fe removal. Similarly, it is important to remember that these results cannot be extended to all RR and conventional soybean cultivars.

3.2 Variety x Fe-EDDHA rate

Four cultivars (two Fe deficiency resistant, two Fe deficiency susceptible) and six rates of Fe-EDDHA (0, 2.24, 4.48, 6.72, 8.96, and 11.2 kg ha^{-1}) were evaluated at one location in 2002 and six cultivars (two Fe deficiency resistant, two moderately resistant, and two susceptible) were evaluated at two locations in 2003. Visual chlorosis scores recorded at V3 could distinguish resistant from susceptible cultivars only when no Fe-EDDHA was applied, whereas harvest seed [Fe] could discriminate among resistant and susceptible cultivars at all six rates of Fe-EDDHA and in exactly the same order at each level of added Fe chelate (Table 1). Although grain yield increased markedly with added Fe chelate (Fig. 1. C), seed [Fe] changed very little (approx. 11%) (Fig. 1. F). The rank order of cultivars for harvest seed [Fe] was also the same as that of the cultivars' initial or planting seed [Fe], providing some evidence that seed [Fe] reflects varietal differences in resistance to Fe deficiency. Similar results recorded for the two 2003 trials, where two additional cultivars were evaluated under different severities of Fe deficiency, extend the applicability of this concept to evaluations conducted on similar soils.

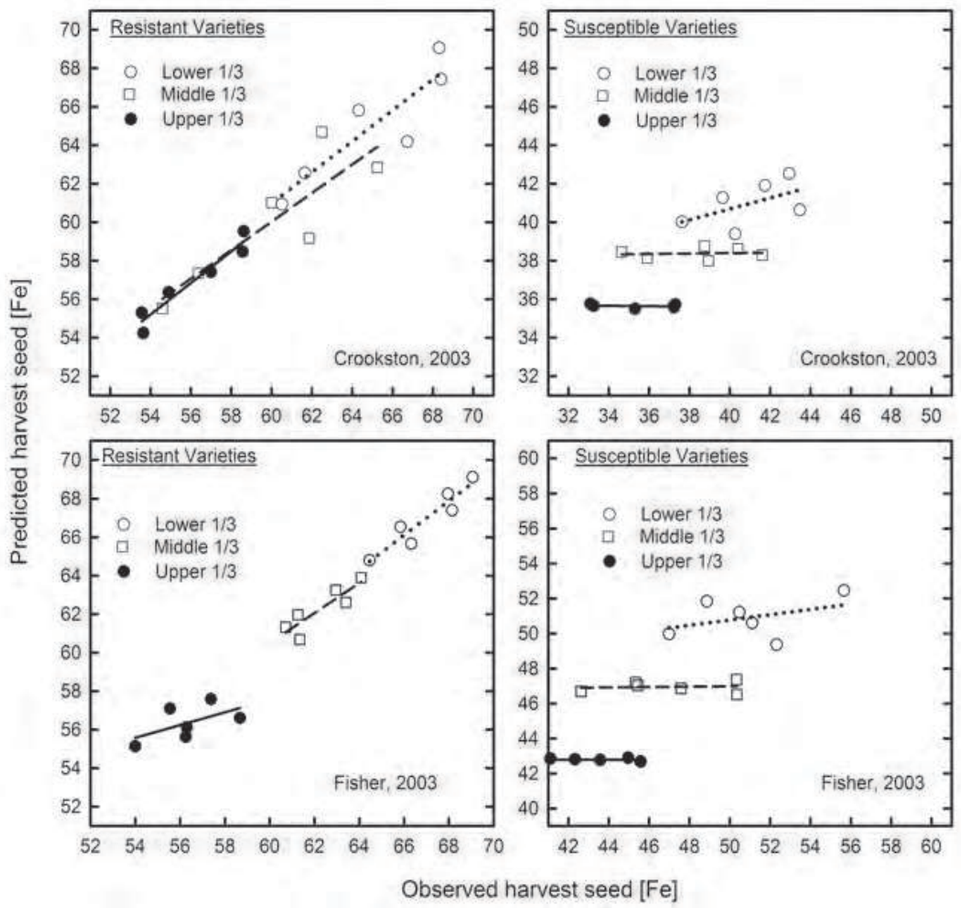

Fig. 4. Results (observed and predicted values) from linear regression equations of harvest seed [Fe] on applied Fe-EDDHA were significant for each one-third of the canopy for resistant cultivars, but for none of the canopy thirds for susceptible cultivars, Crookston, MN and Fisher, MN, 2003. Rates of applied Fe-EDDHA were: 0, 125, 250, 375, 500, 625 mg Fe-EDDHA per m of a 0.56 m wide row.

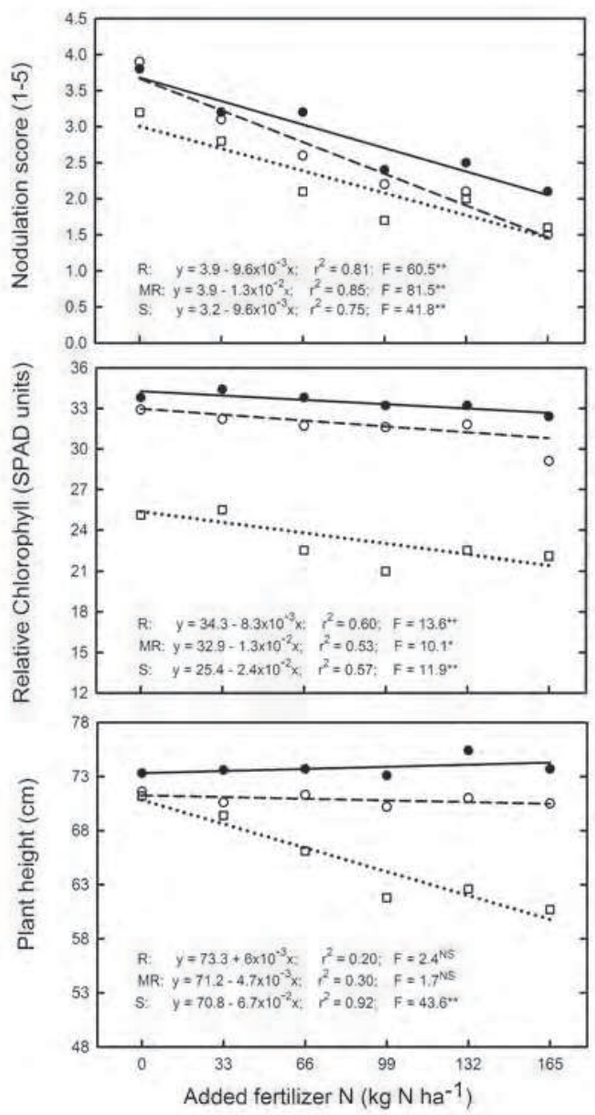

Fig. 5. Varietal differences in linear response to added N, averaged across three years, for plant height, relative chlorophyll, and nodulation score.

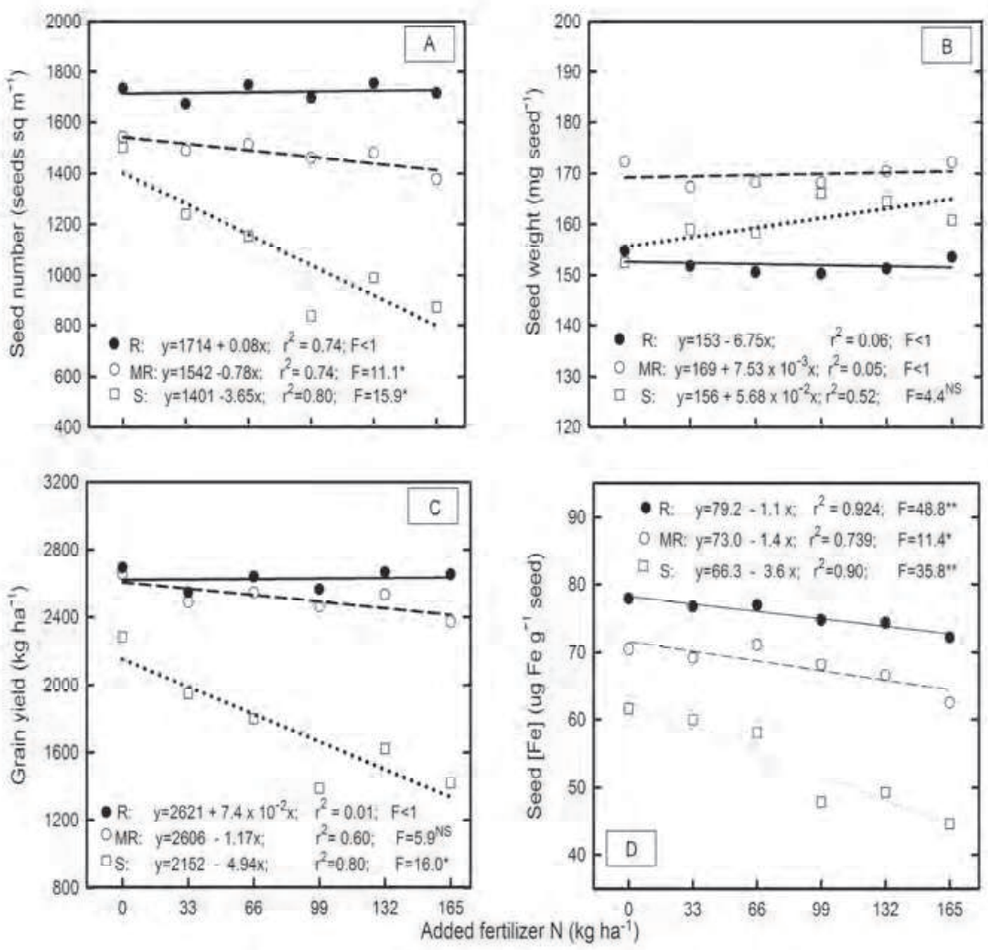

Fig. 6. Varietal differences in linear response to added N, averaged across three years for seed number, seed weight, grain yield, and seed [Fe].

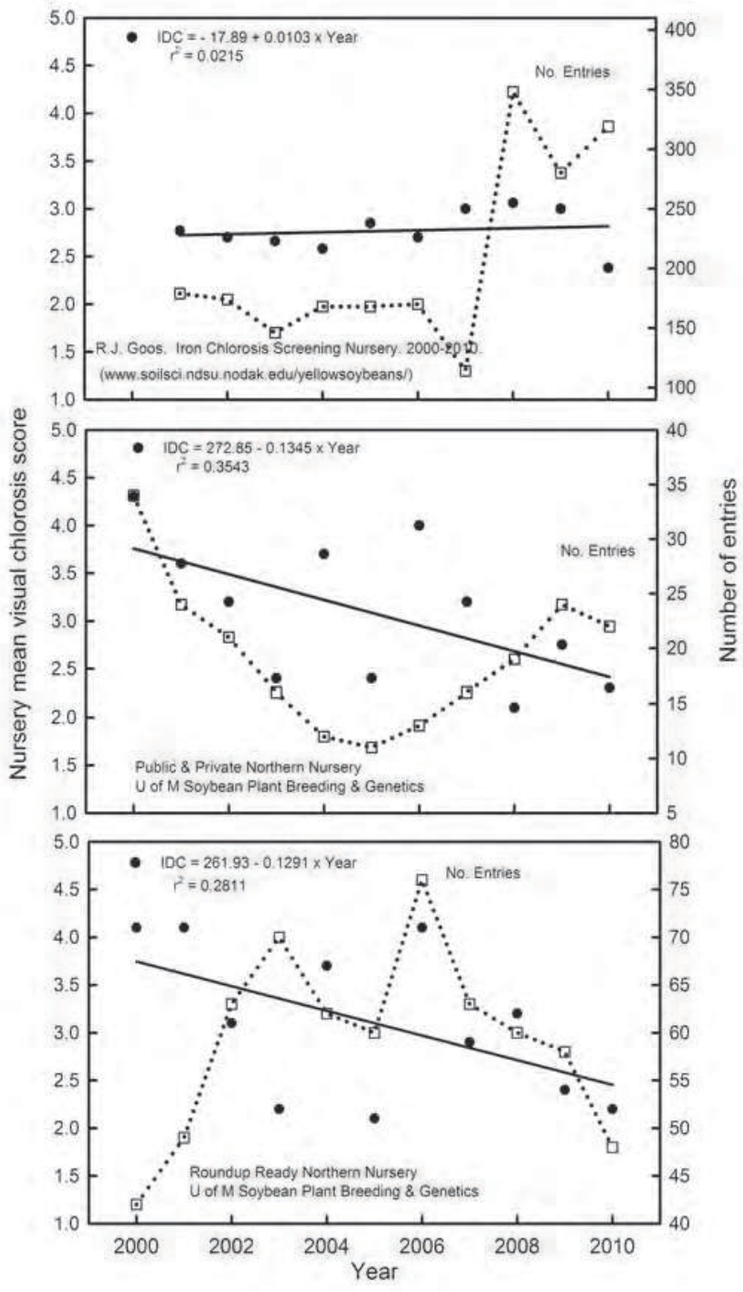

Fig. 7. Changes in means of visual chlorosis score and number of entries during the last decade for three large-scale chlorosis nurseries.

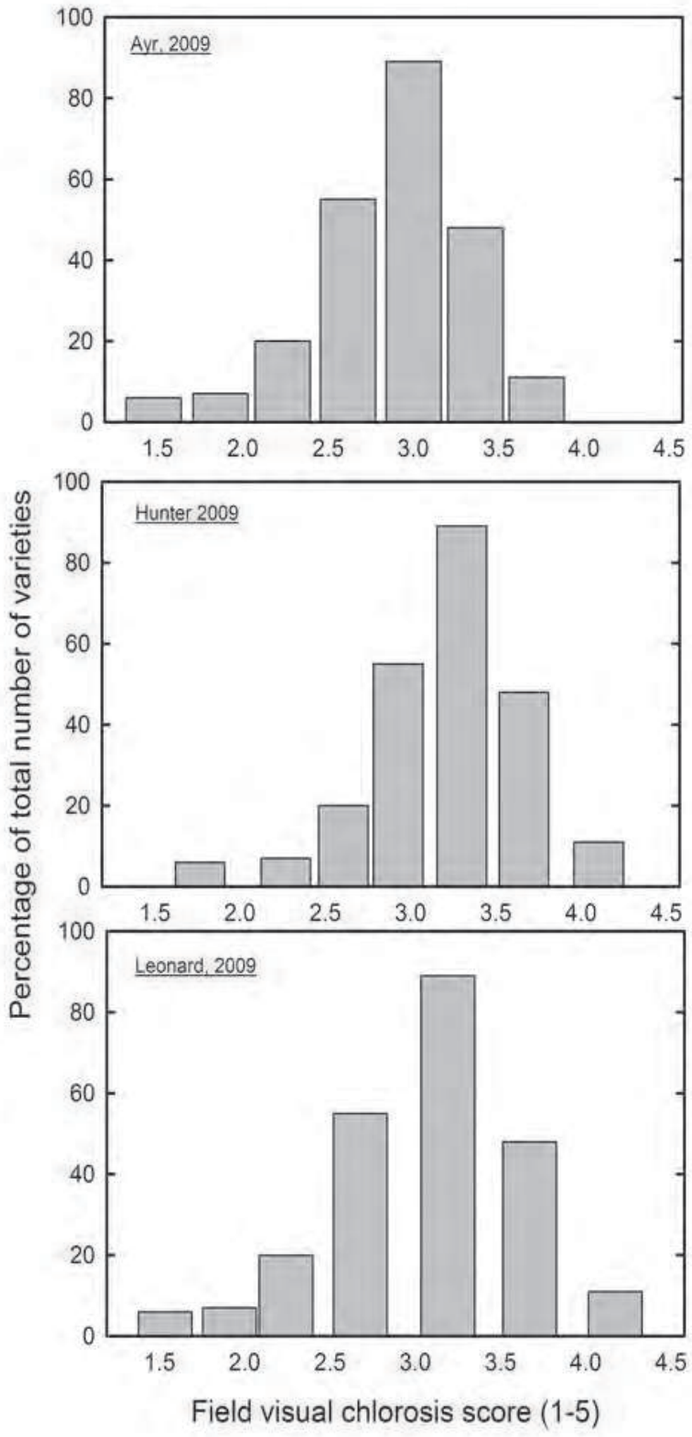

Fig. 8. Frequency (as a percentage of the total) of cultivars in increasing, field visual chlorosis categories at three North Dakota locations in 2009.

Year		Amenia	Ayr	Colfax	Galesburg	Leonard
2008						
	Amenia	1	0.7902**	0.8386**	0.8118**	0.6696**
	Ayr		1	0.7676**	0.7559**	0.6368**
	Colfax			1	0.7958**	0.6832**
	Galesburg				1	0.6372**
	Leonard					1
2009						
		Ayr	Hunter	Leonard		
	Ayr	1	0.7989**	0.7817**		
	Hunter		1	0.7964**		
	Leonard			1		
2010						
		Ayr	Colfax	Galesburg	Leonard	Prosper
	Ayr	1	0.6932**	0.7227**	0.5606**	0.6674**
	Colfax		1	0.5829**	0.5109**	0.6168**
	Galesburg			1	0.5151**	0.5800**
	Leonard				1	0.5270**
	Prosper					1

** Significant at 1% level of probability.

Table 2. Genotypic rank correlations across several North Dakota locations during 2008, 2009, and 2010.

3.3 Northwest Minnesota - seventy-two cultivars, 4 environments

Results from earlier research (Table 1; Figs.1, 2, and 3) provided preliminary, but convincing, evidence that grain yield and harvest seed [Fe] were closely related to planting seed [Fe] across several genotypes when conditions favorable for Fe deficiency prevailed. These studies, however, involved only 4 to 29 cultivars. To confirm this observation we evaluated 72 cultivars expressing a wide range of seed Fe concentrations. Our primary objective was to compare plant traits thought to represent measures of resistance to Fe deficiency. This collection of Maturity Group 00 (MG 00) genotypes had a range of planting seed Fe concentrations from 64 to 106 ug Fe g^{-1} seed. We assumed that the seed we obtained had been grown with adequate Fe availability. Plants were grown in nutrient solution as well as field nurseries. Nutrient solution culture procedures described by Chaney et al. (1992) were used to evaluate genotypes grown with moderate to severe Fe deficiency under controlled conditions. Other researchers have concluded that similar quantitative trait loci (QTL) are identified in nutrient solution and field tests and, therefore, both systems identify similar genetic mechanisms of iron uptake and/or utilization (Lin et al., 2000).

These seventy-two genotypes also were grown on high pH, highly calcareous soils at three locations in 2003 and one location in 2004. Measures of resistance to Fe deficiency were: harvest seed [Fe] (µg g^{-1} seed); harvest seed Fe content (µg 1000^{-1} seeds); and Fe removal (µg Fe m^{-2}). Classification variables were: published visual chlorosis (VC); in-field visual chlorosis at V3 (V3); planting seed [Fe] (µg Fe g^{-1} seed) (FC); planting seed Fe content (µg Fe 1000^{-1} seeds) (FS); and relative chlorophyll concentration (SPAD values) (GC).

Type 3 Tests of Fixed Effects

Effect	Numerator df	Denominator df	F value	Pr > F
Fe Rate	1	6	20.83	0.0038
Entry	19	114	4.49	<.0001
Fe Rate * Entry	19	114	0.67	0.8369

Estimates

Label	Estimates	Standard Error	df	t Value	Pr > F
Mean High Rate	35.0325	0.7198	6	48.67	<.0001
Mean Low Rate	30.3862	0.7198	6	42.22	<.0001
HI vs Low Fe	4.6463	1.0179	6	4.56	0.0038
RR	33.8887	0.5781	9.94	58.62	<.0001
Conv.	31.5300	0.5781	9.94	54.54	<.0001
RR vs Conv.	2.3588	0.5482	114	4.30	<.0001
Rate 1 – RR	31.8850	0.8175	9.94	39.00	<.0001
Rate 2 – RR	35.8925	0.8175	9.94	43.90	<.0001
R1 vs R2 – RR	-4.0075	1.1562	9.94	-3.47	0.0061
Rate 1 – Conv.	28.8875	0.8175	9.94	35.34	<.0001
Rate 2 – Conv.	34.1725	0.8175	9.94	41.80	<.0001
R1 vs R2 – Conv.	-5.2850	1.1562	9.94	-4.57	0.0010

Contrasts

Label	Numerator df	Denominator df	F value	Pr > F
Hi vs Low Fe (C1)	1	6	20.83	0.0038
RR vs Conv. (C2)	1	114	18.51	<.0001
C1 x C2	1	114	1.36	0.2464

† SPAD values are described as consistent and accurate measures of leaf chlorophyll content (umoles m^{-2} of leaf area) (Markwell, et al., 1995; Markwell and Blevins, 1999).

Table 3. Analysis of variance of SPAD† at V3 for 10 RR and 10 conventional soybean cultivars grown at two rates of Fe-EDDHA under severe Fe deficiency.

Type 3 Tests of Fixed Effects

Effect	Numerator df	Denominator df	F value	Pr > F
Fe Rate	1	6	1.54	0.2614
Entry	19	114	2.37	0.0026
Fe Rate*Entry	19	114	0.61	0.8950

Estimates

Label	Estimates	Standard error	df	t value	Pr. [t]
Mean High Rate	2797.27	247.64	6	11.30	<.0001
Mean Low Rate	2363.11	247.64	6	9.54	<.0001
HI vs LOW Fe	434.16	350.21	6	1.24	0.2614
RR	2806.51	181.92	6.99	15.43	<.0001
Conv.	2353.87	181.92	6.99	12.94	<.0001
RR vs Conv.	452.64	98.65	114	4.59	<.0001
Rate 1 – RR	2568.48	257.27	6.99	9.98	<.0001
Rate 2 – RR	3044.55	257.27	6.99	11.83	<.0001
R1 vs R2 – RR	-476.07	363.84	6.99	-1.31	0.2321
Rate 1 – Conv.	2157.75	257.27	6.99	8.39	<.0001
Rate 2 – Conv.	2550.00	257.27	6.99	9.91	<.0001
R1 vs R2 – Conv.	-392.25	363.84	6.99	-1.08	0.3168

Contrasts

Label	Numerator df	Denominator df	F value	Pr > F
Hi vs Low Fe (C1)	1	6	1.54	0.2614
RR vs Conv. (C2)	1	114	21.05	<.0001
C1 x C2	1	114		0.6717

Table 4. Analysis of variance of grain yield for 10 RR and 10 conventional soybean cultivars grown at two rates of Fe-EDDHA under severe Fe deficiency.

We acknowledge that in our studies genotype and seed [Fe] are confounded and that Fe availability, as well as genotype, likely will influence final seed [Fe]. Although seed [Fe] and genotype are confounded, this is not unlike visual chlorosis score and genotype. A better approach would have been to use several genotypes each having a range of seed [Fe] from 50 to 120 μg g^{-1} seed. We were unable to identify or create these treatments. Nonetheless, we know from earlier research (Wiersma, 2005, 2007, and 2010) that large (25-50%) differences in agronomic performance, within the same genotype, often are associated with rather small (5-10%) differences in harvest seed [Fe]. In this case, correlations among agronomic characters and seed [Fe] are relatively small ($r < 0.4$). We also know from field experiments that differences between cultivars of <10 μg Fe g^{-1} seed are not likely to be statistically significant (Wiersma, 2005, 2007,and 2010). Similarly, Shen et al. (2002) concluded that in wheat "In fact, it is impossible to distinguish completely the role of the genotype vs seed Fe content in the early response to Fe deficiency because the difference in seed Fe content can be an aspect of genotypic difference to Fe deficiency". It is reasonable to think that seed [Fe], seed Fe content, or Fe removal can also be considered aspects of genotypic differences in response to Fe deficiency.

	Year		
Year	2007	2008	2009
2007	1	0.6176*	0.5472*
2008		1	0.3714^{NS}
2009			1

*, NS Significant at 5% level of probability, and not significant at 5% level of probability

Table 5. Genotypic rank correlations of 14 genotypes across several North Dakota locations during 2007, 2008, and 2009.

In-field visual chlorosis is better predicted using at planting seed [Fe] than the recorded visual chlorosis score, although the relationship is far from perfect. The complexity of using individual genotype means, without first classifying them into groups, is illustrated in Fig. 9. The extent of yellowing (VCS) among plots within a nursery often approaches a continuous distribution from green to yellow. Historically, this range of expression has been sub-divided into classes prior to analysis (Fehr, 1982). Thus, to evaluate relationships among characters, the 72 genotypes in each environment were first divided into 5 classes on the basis of several characters: recorded visual chlorosis (VC); visual chlorosis at V3 (V3); seed Fe concentration (FC); seed Fe content (FS); and growth chamber SPAD (GC). Then, Levene's F test (Littell et al., 2006) was used to assess homogeneity of error variances across classes for each measure used in classifying genotypes. Welch's F test was used to test the equality of means across the levels of the single class terms (Littell et al., 2006). Ideally, plant traits used to classify genotypes would have homogeneous error variances (non-significant Levene's F) and significant differences among class means (significant Welch's F).

Classifying genotypes on the basis of visual observations, either VC or V3, rarely (16%) yielded homogeneous class variances, although differences among class means were almost always (83%) significant (Table 6). The heterogeneous class variances indicate that VCSs may not be the most appropriate measures of Fe efficiency and suggest that the slow

improvement in genotypic resistance mentioned earlier may be related to the plant trait used to measure resistance.

Classifying genotypes on the basis of relative chlorophyll concentration (GC) yielded homogeneous class variances; however, differences among class means were not statistically significant (Table 6). The severity of Fe chlorosis in nutrient solution culture was especially harsh and may have limited genotypic expression of resistance to those genotypes having high Fe-efficiency (Jessen, et al., 1988). Although other researchers have concluded that similar QTL for visual chlorosis are identified in nutrient solution and field tests (Lin et al., 2000), other QTL may be identified when integrated measures of resistance, manifest at maturity, are evaluated.

Classifying genotypes on the basis of planting seed Fe content (ng Fe $seed^{-1}$ or ug Fe 1000^{-1} seeds) resulted in homogeneous class variances for each measure of resistance, whereas, differences among class means were significant only for harvest seed Fe content (Table 6; Fig. 10). Measures of planting seed Fe content should provide reliable measures of resistance to Fe deficiency defined as Fe accumulation. Using planting seed [Fe] to classify genotypes resulted in homogeneous class variances for Fe accumulation and harvest seed [Fe], but not for Fe removal. Differences among class means were significant for each measure of resistance. The heterogeneous class variances for Fe removal is a warning that planting seed [Fe] may not provide consistent, reliable estimates of resistance to Fe deficiency defined as Fe removal at harvest. Another interpretation is that Fe removal at harvest may not be an acceptable measure of resistance to Fe deficiency because it involves the primary yield component, seeds m^{-2}. Grain yield is not necessarily a suitable measure of resistance to Fe deficiency, especially where Fe is not yield-limiting, such as on non-IDC prone sites (Helms, et al., 2010). Helms, et al. (2010) also noted that visual chlorosis scores could not identify the highest-yielding genotype even where Fe was yield-limiting.

The severity of Fe deficiency among environments ranged from almost no chlorosis (Fisher, MN, 2003; VCS=1.2) to mild chlorosis (Crookston, MN, 2003; VCS=2.3) to moderate chlorosis (Ada, MN, 2003; VCS=3.0) to severe chlorosis (Crookston, MN, 2004; VCS=4.2). Across this wide range of IDC severity, our results emphasize the difficulty of identifying superior genotypes when visual observations, either VC or V3, are used to classify genotypes, whereas, the importance of seed [Fe] for efficient genotype selection (consistency and reliability) is underscored. Genotypes were also ranked in each environment for three putative measures of resistance to Fe deficiency and for four classification variables thought to represent potential measures of resistance to Fe deficiency. These values were then correlated to determine genotypic rank correlations among environments (Table 7).

When genotypes were ranked using published visual chlorosis scores or in-field visual chlorosis scores, there was little association with measures of resistance to Fe deficiency. In contrast, when genotypes were ranked using planting seed [Fe] or planting seed Fe content, there often was a close association with measures of resistance to Fe deficiency. These generalizations, however, do not include Crookston, 2004 where IDC was especially severe and some genotypes barely survived. Nonetheless, planting seed [Fe] and content are substantially superior to measures of visual chlorosis for identifying consistent, reliable estimates of resistance to Fe deficiency (Fig. 10). The consistency and reliability of using seed [Fe] as a measure of resistance to Fe deficiency in soybean is further illustrated in the article written by Spehar (1994).

Using results from this study of 45 cultivars of soybean grown on partly- and fully-limed acid soils in Brazil, it is possible to calculate a genotypic rank correlation coefficient

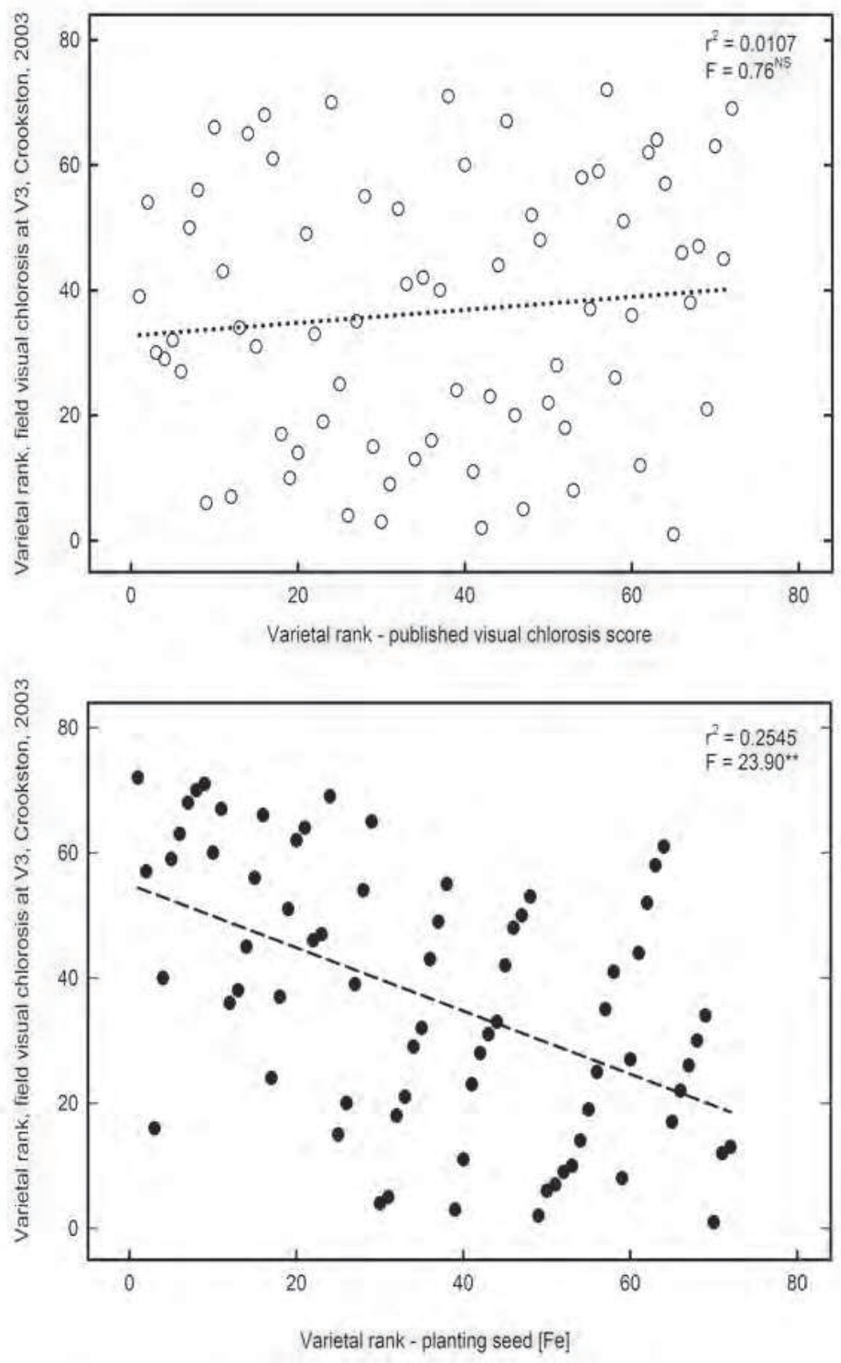

Fig. 9. Regression of varietal rank for visual chlorosis at V3 on varietal rank for published visual chlorosis score (VC) and planting seed [Fe].

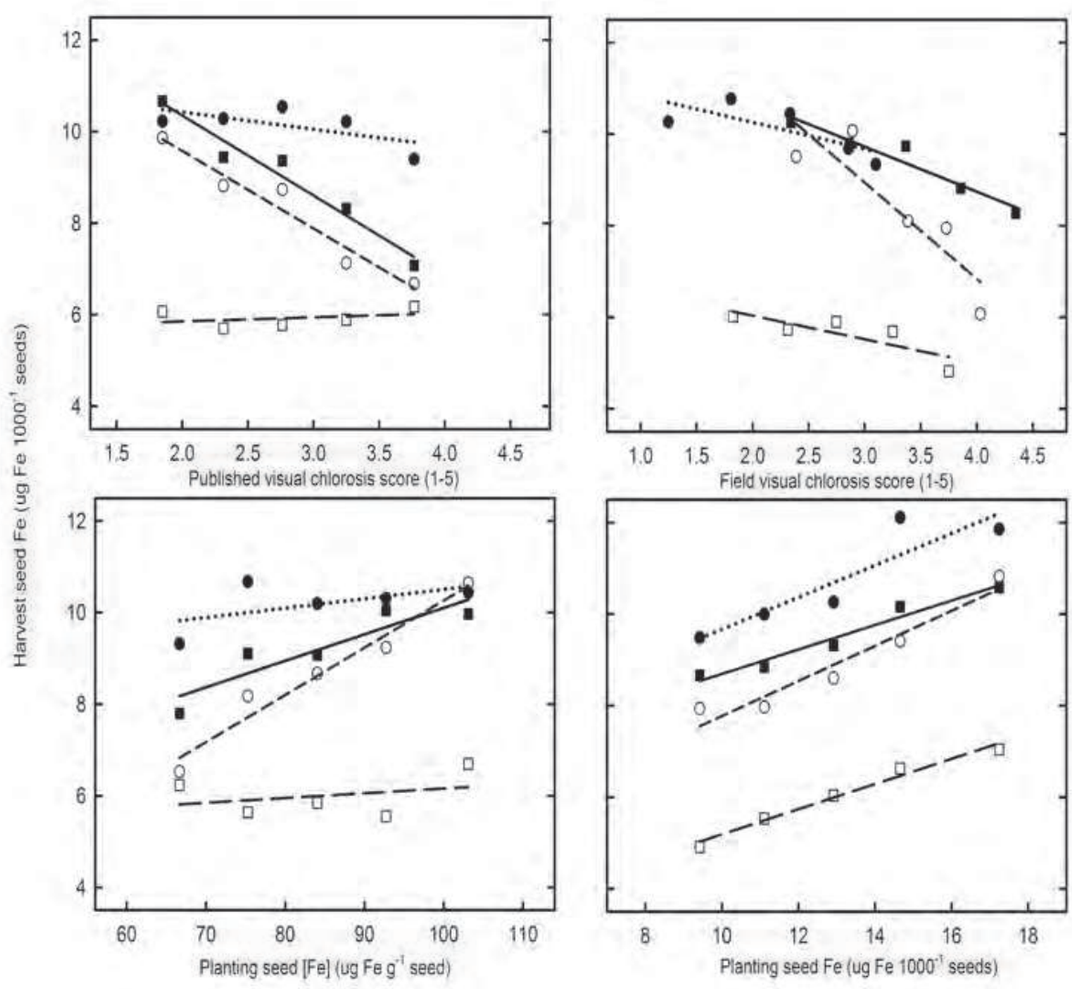

Fig. 10. Relationships between seed Fe content at harvest and four classification variables. Each regression equation is represented by the same symbol and line type for each environment in each panel: filled circle, dotted line is Fisher, MN, 2003; filled square, solid line is Ada, MN, 2003; open circle, short dash line is Crookston, MN, 2003; open square, long dash line is Crookston, MN, 2004.

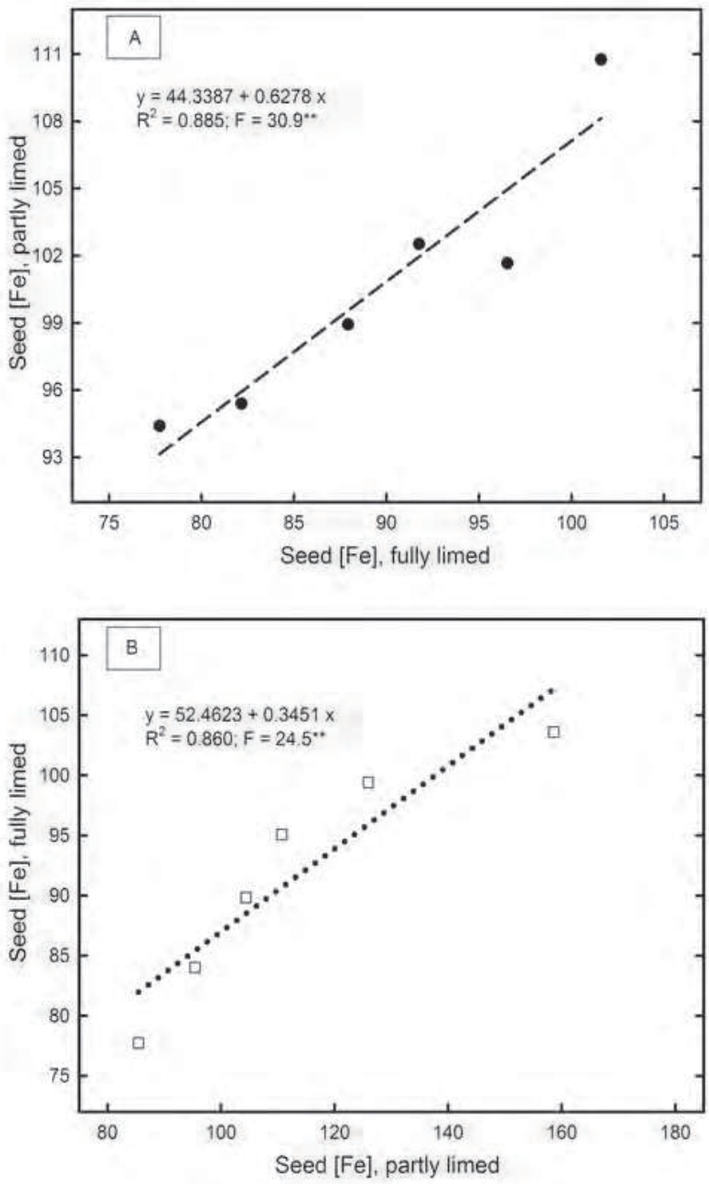

Fig. 11. Seed [Fe] determined from genotypes grown on fully-limed acid soils can be used to predict seed [Fe] of those same genotypes when grown on partly-limed soils (A); similarly, seed [Fe] determined from genotypes grown on partly-limed soils can be used to predict seed [Fe] of those same genotypes when grown on fully-limed soils (B).

Classification variable	Measure of resistance	Mean†	Standard deviation‡	Levene's F§	Welch's F¶
Published visual chlorosis score (VC)	ug Fe 1000^{-1} seeds	VC1=9.2 VC2=8.5 VC3=8.6 VC4=7.9 VC5=7.3	VC1=9.2 VC2=8.5 VC3=8.6 VC4=7.9 VC5=7.3	<1.0^{NS}	2.36^{NS}
	ug Fe g^{-1} seed	VC1=74.7 VC2=70.3 VC3=64.7 VC4=62.0 VC5=59.8	VC1=19.3 VC2=20.2 VC3=17.5 VC4=14.9 VC5=13.2	5.01**	3.66*
	Fe removal (ug Fe m^{-2})	VC1=10.6 VC2= 9.5 VC3= 8.2 VC4= 6.6 VC5= 6.0	VC1=3.7 VC2=3.7 VC3=2.8 VC4=2.0 VC5=1.4	9.02**	12.68**
Field visual chlorosis (V3)	ug Fe 1000^{-1} seeds	V31=9.9 V32=8.0 V33=8.5 V34=8.2 V35=7.9	V31=1.8 V32=2.5 V33=2.4 V34=1.8 V35=2.3	3.16*	7.50**
	ug Fe g^{-1} seed	V31=82.8 V32=62.7 V33=66.6 V34=63.9 V35=63.6	V31=13.4 V32=20.5 V33=20.1 V34=14.3 V35=13.6	18.42**	14.71**
	Fe removal (ug Fe m^{-2})	V31=5.6 V32=7.6 V33=9.8 V34=8.4 V35=7.2	V31=0.4 V32=3.3 V33=3.7 V34=2.6 V35=3.3	3.42**	21.87**
Planting seed [Fe] (FC)	ug Fe 1000^{-1} seeds	FC1=7.5 FC2=8.4 FC3=8.4 FC4=8.8 FC5=9.4	FC1=2.2 FC2=2.3 FC3=2.1 FC4=2.4 FC5=2.0	<1.0^{NS}	2.89*
	ug Fe g^{-1} seed	FC1=55.6 FC2=64.5 FC3=69.0 FC4=72.2 FC5=75.8	FC1=14.6 FC2=17.4 FC3=18.2 FC4=19.7 FC5=18.6	1.88^{NS}	7.16**
	Fe removal (ug Fe m^{-2})	FC1=7.0 FC2=7.9 FC3=8.6 FC4=9.5 FC5=10.6	FC1=2.4 FC2=2.8 FC3=3.5 FC4=4.0 FC5=3.5	5.01**	4.24**

Classification variable	Measure of resistance	Mean†	Standard deviation‡	Levene's F§	Welch's F¶
Planting seed Fe content (FS)	ug Fe 1000^{-1} seeds	FS1=7.7 FS2=8.1 FS3=8.6 FS4=9.6 FS5=10.1	FS1=2.0 FS2=2.4 FS3=2.1 FS4=2.6 FS5=2.1	1.59^{NS}	5.63**
	ug Fe g^{-1} seed	FS1=67.6 FS2=64.9 FS3=68.0 FS4=66.3 FS5=71.8	FS1=18.4 FS2=18.4 FS3=19.2 FS4=17.1 FS5=18.8	$<1.0^{NS}$	$<1.0^{NS}$
	Fe removal (ug Fe m^{-2})	FS1=8.4 FS2=8.0 FS3=8.7 FS4=8.3 FS5=10.4	FS1=3.2 FS2=3.2 FS3=3.5 FS4=3.2 FS5=3.3	$<1.0^{NS}$	1.49^{NS}
Relative chlorophyll concentration SPAD (GC)	ug Fe 1000^{-1} seeds	GC1=8.2 GC2=8.0 GC3=9.0 GC4=8.7 GC5=9.9	GC1=2.2 GC2=2.3 GC3=2.5 GC4=2.2 GC5=2.6	$<1.0^{NS}$	$<1.0^{NS}$
	ug Fe g^{-1} seed	GC1=66.3 GC2=64.6 GC3=69.3 GC4=80.6 GC5=80.0	GC1=17.7 GC2=18.3 GC3=17.8 GC4=20.6 GC5=24.8	$<1.0^{NS}$	$<2.45^{NS}$
	Fe removal (ug Fe m^{-2})	GC1=8.4 GC2=8.0 GC3=9.1 GC4=10.9 GC5=11.4	GC1=3.1 GC2=3.1 GC3=3.8 GC4=4.3 GC5=4.7	1.77^{NS}	1.65^{NS}

† Mean of resistance measure for each level of classification.
‡ Standard deviation of resistance measure for each level of classification.
§ Test to assess homogeneity of error variances across levels of classification
¶ Test to assess the equality of classification means.
^{NS}, *, ** Not significant at 5% level of probability, significant at 5% level of probability, and significant at 1% level of probability.

Table 6. Classification of genotypes into 5 levels of selected plant traits thought to represent measures of resistance to Fe deficiency, defined as Fe accumulation (ug Fe 1000^{-1} seeds), harvest seed [Fe] (ug Fe g^{-1} seed), and Fe removal (ug Fe m^{-2}).

between partially- and fully-limed conditions of r=0 .686 (P<0.001) using nearly all genotypes. However, some genotypes were missing seed [Fe]s under one treatment or another and 7 cultivars were not included in later calculations. Using 38 genotypes and 6 seed [Fe] classes (5 ppm), seed [Fe] on partly-limed soil could be predicted from seed [Fe] on fully-limed soil: linear, r^2=0.883, F=30.2** (Fig. 11, A). Using 38 genotypes and 6 seed [Fe] classes (10 ppm), seed [Fe] on fully-limed soil could be predicted from seed [Fe] on partly-

limed soil: linear, r^2=0.860, F=24.5** (Fig. 11, B). Differences in class sizes (5 vs 10 ppm) are related to the range of seed [Fe] values observed for the independent variable. Nonetheless, the same genotypes usually were included in the same classes whether based on 5 or 10 ppm, which led to nearly identical results.

Presuming that seed [Fe] can be regarded as an integrated measure of resistance to Fe deficiency that is manifest at maturity, then Spehar's data provides additional evidence that individual genotypes have a seed [Fe] "threshold" that is genetically predetermined, yet seldom exceeded, and that seed [Fe] should supplement or replace VCS as a measure of resistance to Fe deficiency.

		Measures of resistance to Fe deficiency		
Environment	Classification variable	Harvest seed [Fe] (ug Fe g^{-1} seed)	Harvest Fe content (ug Fe 1000^{-1} seeds)	Fe removal (ug Fe m^{-2})
Ada, 2003	VC†	-0.2464*	-0.2007^{NS}	-0.0254^{NS}
	V3	-0.0984^{NS}	-0.0137^{NS}	0.1932^{NS}
	FE	0.4382**	-0.2505*	0.3687**
	FS	0.3454**	0.1730^{NS}	0.3646**
Crookston, 2003	VC	-0.2214^{NS}	-0.0554^{NS}	0.0186^{NS}
	V3	-0.3616**	-0.3838**	-0.1832^{NS}
	FE	0.5698**	0.4548**	0.4402**
	FC	0.1701^{NS}	0.4038**	0.2148^{NS}
Fisher, 2003	VC	-0.1722^{NS}	-0.0659^{NS}	.‡
	V3	-0.0999^{NS}	0.0722^{NS}	.
	FE	0.3568**	0.0975^{NS}	.
	FC	0.2468*	-0.0057^{NS}	.
Crookston, 2004	VC	-0.1282^{NS}	0.0320^{NS}	-0.0099^{NS}
	V3	-0.1158^{NS}	-0.0887^{NS}	-0.1048^{NS}
	FE	0.2211 ^{NS}	-0.0298^{NS}	0.0482^{NS}
	FC	0.0044^{NS}	-0.0950^{NS}	-0.0365^{NS}

† VC, V3, FE, and FC are published visual chlorosis score, in-field visual chlorosis score, planting seed [Fe], and planting seed Fe content.
‡ Missing data.

Table 7. Correlations among genotypes, across four environments, ranked on the basis of three measures of resistance to Fe deficiency and genotypes ranked on the basis of four classification variables though to represent potential measures of resistance to Fe deficiency.

4. Conclusions

Conclusions from the research discussed in this chapter are: (1) soybean seed [Fe] and/or seed Fe content provide reliable and consistent measures of genetic differences in resistance to Fe deficiency; (2) seed [Fe] is tightly controlled genetically; (3) it is not likely that

susceptible genotypes will accumulate high seed [Fe] even when excess Fe is available; (4) seed [Fe] or content at harvest, more so than VCS, can also reflect responses to management practices designed to reduce or alleviate Fe deficiency; (5) when soybean is grown on chlorosis-prone soils, increasing seeding density can markedly increase grain yield and seed [Fe] of both susceptible and resistant cultivars, whereas applying higher rates of Fe-EDDHA especially benefits susceptible cultivars; (6) increasing rates of added fertilizer nitrate have little influence on Fe deficiency of resistant cultivars, but severely depress plant height, grain yield and harvest seed [Fe] of susceptible cultivars; (7) genotypic rank correlations of visual chlorosis scores across locations within a year are reasonably consistent and reliable; however, rank correlations across years are not; (8) classifying genotypes using VCS can result in heterogeneous class variances indicating that VCSs may not be appropriate (consistent, reliable) measures of Fe efficiency; (9) measures of genetic resistance to Fe deficiency should include measures of seed [Fe] or content; and (10) the slow improvement in genotypic resistance to Fe deficiency may be related to the plant trait used to measure resistance.

Seed [Fe] is very useful for identifying superior genotypes in management and agronomic performance trials; it also provides a consistent, reliable estimate of resistance to Fe deficiency, thereby enhancing genotype selection.

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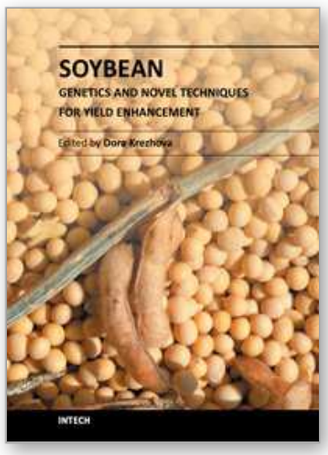

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